run towards the opposite end. The centre chains of cellulose I_β have similar hydrogen-bond strings, continuous in each direction[2]. In the origin chains, the hydrogen bonding is either straight across from chain to chain, or solely intramolecular so that adjacent chains are not linked.

The long strings of hydrogen bonds are structurally reminiscent of linear hydrogen-bonding systems seen in protein-bound water ('proton wires')[7]. Cellulose is much more rigid than bound water, though[5]. A question that Nishiyama *et al.*[1,2] could not answer was whether the alternative hydrogen-bond networks can interconvert cooperatively in time, as required for proton conduction in water[7], or whether they are permanent but distributed in space within or between microfibrils. This question is fundamental for cellulose I_β, where the sheets of origin chains lack cohesion if hydrogen bonding in the centre chains is polarized in one of the two possible directions.

Cellulose is synthesized at the cell surface by membrane-spanning synthase complexes. These take the form of regular arrays of particles in most algae[8] and hexameric rosettes in higher plants, with each rosette containing cellulose synthase enzymes of three distinct kinds[9]. Is it the geometry of these arrays and rosettes, or self-assembly, that determines the structure of cellulose microfibrils? Both, it seems. The lateral dimensions of microfibrils vary with the size of the arrays[8,10], and in each microfibril the chains are parallel (heads all pointing the same way) because that is how they emerge from the synthetic complex.

How the terminal complexes fit together is influenced by the sequence of the cellulose synthases[9,10]. If the internal structure of each microfibril were templated by its terminal complex, we should expect aberrant crystalline cellulose structures to result from mutations disrupting the complex. So far no such aberrations have been described, suggesting that the cellulose I_α and I_β lattices self-assemble. But there is a twist to this tale. In the model plant *Arabidopsis*, a single amino-acid substitution in one of the cellulose synthases interferes with rosette assembly and is sufficient to disrupt ordered orientation of the microfibrils[11]. The resulting plants are dwarfed, apparently through disorientation of microfibrils that would normally be wrapped around the cells of plant stems to constrain them into elongating rather than expanding equally in all directions. This is not the only factor influencing the direction of growth, but normal synthesis of cellulose seems to be needed for the normal development of plant form.

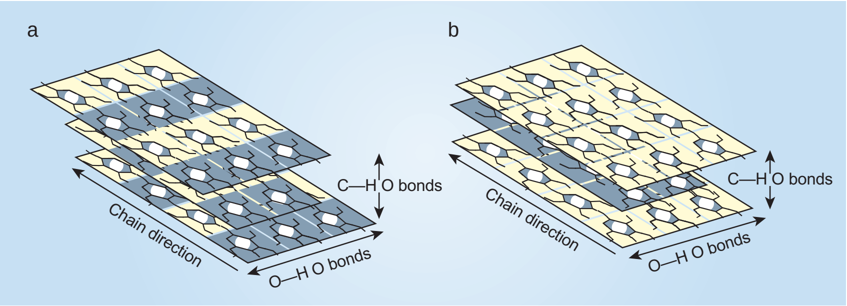

Figure 2 **Symmetry and directions of hydrogen bonding in cellulose[1,2].** a, **Cellulose I_α, in which all chains are crystallographically identical but alternating glucose units in each chain, shaded grey and yellow, differ slightly in conformation.** b, **Cellulose I_β, in which chains of two distinct kinds are arranged in alternating sheets. Chains passing through the origin and centre of the unit cell are shaded respectively yellow and grey.**

The new structures do not close the debate on the nature of cellulose. Is their unexpected complexity random, the consequence of imprecise self-assembly? Or is it the result of spatial patterning by the geometry of the terminal complexes, so that understanding structural detail and biosynthesis will have to go hand in hand? Could the hydrogen-bond networks be switchable? If they are, cellulose is a smarter material than anyone thought. ■

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Geomorphology

Nature, nurture and landscape

Peter Molnar

Those studying erosion in mountain regions wrestle with factors such as what builds mountains, and how climate affects erosive forces. Yet perhaps a physically based theory is what most needed.

The endless debate over the relative importance of nature and nurture in child development has its equivalent in geomorphology. In this case, the argument is about the roles of tectonics and climate in mountain erosion. Tectonics (nature) sets the initial conditions by raising Earth's surface and, where active, renewing topography. Climate (nurture) shapes the surface into its various forms through its effect on glaciers and rivers. Three papers in this issue[1–3] and another in *Geology*[4] take the argument forward by isolating and evaluating the importance of certain climatic and tectonic factors in erosion.

As well as offering individual insights, these papers show how lack of resolution in the debate is impelling research in geomorphology away from observation and towards theory. Moreover, in different ways, they remind us that understanding the physical processes that govern the most pervasive of erosive forces, river erosion, requires a geological approach to provide data way back in time. Although there is a long tradition of measuring sediment transport by rivers, only infrequently will that record include the full range of floods that have shaped the landscape. Flooding obeys a power-law distribution[5], and the largest floods have the largest effect on landscape. But only in rare regions are we likely to have witnessed them — hence the need for an approach that will produce a record that includes several such extreme events.

To quantify erosion rates, all four groups[1–4] apply thermochronometric methods to rock now exposed at the surface. Temperature increases with depth in the Earth and, at high temperatures, noble gases emitted in radioactive decay diffuse away; defects (tracks) in crystals, produced by the charged particles expelled in nuclear fission, anneal. By measuring the concentrations of such gases or tracks, one can date when the sample cooled below a temperature at which diffusion or annealing is slow. With an assumed temperature gradient in the Earth, the upshot is an estimate of the average exhumation rate, which in these cases equals the rate that material above the sampled rock has been eroded. Such estimates apply to periods as short as 500,000 years to as long as several million years. But in all cases they span several glacial and interglacial cycles, and so smooth the effects of large climatic changes.

Reiners *et al.*[1] present the simplest result: erosion rates averaged over the past few million years in the North Cascade Mountains of Washington state correlate with the present-day distribution of rainfall. Precipitation and erosion rates vary by an order of magnitude across the range, with rapid erosion having occurred where rain falls most today. As virtually all of the rock exposed in the mountains must have lain below sea level a few million years ago, they deduce that rock moved up relative to sea level despite the absence of any tectonic process. Because of isostasy (Archimedes' principle applied to the Earth's crust immersed in its more dense mantle)[1,6], removal of a mass of rock from the Earth's surface will be compensated by the rise above sea level of approximately 80–85% of that mass.

By contrast, Burbank *et al.*[2] deny that precipitation has a major role in erosion in their study area, the Himalaya. They measured rainfall along a profile across a segment of the Himalaya, and they compare that rainfall with estimates of erosion rates along a valley floor from the Lesser Himalaya into the Greater Himalaya. A narrow zone separates the Lesser Himalaya (where wide rivers, bounded by sediment-filled terraces, flow through relatively gentle, deeply weathered hillslopes) from the snow-capped Greater Himalaya (where slopes are steep, valleys deep, and weathering and terraces sparse).

Burbank *et al.* measured much more rapid erosion in the Greater than the Lesser Himalaya. More importantly, they detected no measurable difference in erosion rates across the Greater Himalaya despite a five-fold decrease in precipitation there. They infer that precipitation does not exert a first-order control on erosion. Noting that all of the rapidly eroding terrain moves rapidly upward with respect to the lower, gentler region to the south, and leaving open the question of what physical processes cause erosion, Burbank *et al.* suggest that tectonically forced upward movement is the most important factor affecting erosion across a region of such different rainfall.

Using a different thermochronometer, spanning several million years, Wobus *et al.*[4] deduce average erosion rates in a neighbouring part of Nepal. Like Burbank *et al.*, these authors report a large difference between high erosion rates in the Greater Himalaya and low rates in the Lesser Himalaya. Because their thermochronometer applies to a much longer period of time, their results require a larger difference in the amount of rock eroded. Only a few kilometres of rock have been removed from the Lesser Himalaya since the Himalaya began to form some 40–50 million years ago, but in the Greater Himalaya roughly 10 km have been removed since about 10 million years ago. There is no obvious fault or shear zone between them, but Wobus *et al.* logically deduce that the rock in the Greater Himalaya has moved upwards relative to that in the Lesser Himalaya. Whereas Burbank *et al.* attribute the constant erosion rates across the Greater Himalaya to rapid rates of vertical movement of the rock, Wobus *et al.* suggest the opposite: that the rapid rise of Greater Himalayan rock results from its rapid erosion and isostatic compensation of the mass removed.

Common to these three papers[1,2,4] is the sensible assumption that the landscapes studied have reached some form of equilibrium, so that the basic character of the landscape and the rates at which geomorphological processes have shaped it have not changed over the time spanned by the measured erosion.

For their part, Dadson *et al.*[3] examined

Figure 1 **Peak erosion — one of the areas of Taiwan studied by Dadson *et al.*[3]. They conclude that these peaks have been stripped of material by earthquake-triggered landslides. (Photo courtesy of J. C. Lin, National Taiwan Univ.)**

100 YEARS AGO

For some years a very interesting series of experiments in connection with the biological method of sewage treatment has been carried on by Dr. Dunbar, director of the Hygienisches Institut at Hamburg, and by his colleagues. Special attention has been directed to the elucidation of the sequence of changes which underlies the purification process in contact beds and percolating filters… Great importance is attached by the Hamburg workers to the role played by the process of so-called "absorption" which takes place when the liquid is in contact with the purifying medium. It has been found that sterile clinkers have the power of withdrawing from solution not only colouring matters, but also the highly complex nitrogenous bodies found in sewage… An interesting example of absorption is seen in the case of the percolating filter adopted by Dr. Dunbar. This filter is provided with a layer of fine material on the surface about six inches deep. According to Dr. Dunbar, 50 per cent. of the purification, apart from nitrification, takes place in this six inches.

From *Nature* 10 December 1903.

50 YEARS AGO

In case there is any lingering doubt that the Piltdown finds are in part fraudulent, we think that one other fact now brought to light should be published immediately. Suspecting that some of the so-called implements reported from the site might have been 'doctored', we asked Mr. E. T. Hall, of the Clarendon Laboratory, Oxford, to test the composition of their surface stains by means of his X-ray spectrographic method of analysis. He has reported to us that the stains on these flints are entirely ferruginous, with one notable exception. The triangular flint (Reg. No. E.606) recovered *in situ* from the layer immediately overlying the skull horizon is chromate stained. When this stain is removed in acid the flint appears greyish-white. It is indistinguishable from a mechanically broken piece of flint such as one might encounter on the surface of any ploughed field in 'Chalk-land'. Whereas a bone might have been dipped in a solution of potassium dichromate with the sole purpose of trying to harden it, a flint would only have been treated in that way by a forger requiring it to be of a certain colour.

From *Nature* 12 December 1953.

erosion of Taiwan at three different timescales. They find both commonality and marked differences in their results. On the oldest rock, where topography is steep, the high erosion rates averaged over the past few million years differ little from those inferred from modern (the past 30 years or less) rates, obtained from ratios of rates of sediment transport by rivers to the areas of their watersheds. On the flanks of the mountainous terrain, where folding and faulting at depth build new topography in weaker rock, present-day erosion rates are highest, despite the low stream gradients and gentle hillslopes, characteristic of slow erosion elsewhere. Moreover, for some of these areas, the average erosion rate obtained from 30 years or so of data exceeds the rates of river incision of narrow valleys over the past 10,000 years. Thus, the modern average erosion rates in these regions cannot have applied to a geological period as short as 10,000 years.

Dadson *et al.* searched for spatial correlations of erosion with factors such as precipitation rate, river discharge, stream gradient and stream power (see below). They conclude that only two correlate well: recent seismicity (Fig. 1), and precipitation associated with typhoons. Earthquakes and large storms are notorious triggers of landslides, which abruptly carry debris to rivers; so these correlations are less surprising than the failure of the other factors. Moreover, the historical record of seismicity on Taiwan goes back only about 100 years, and thus is surely too short to yield a representative image of the distribution of landslide triggers. Perhaps it is no wonder that modern average erosion rates and those averaged over geological times differ in the low parts of Taiwan.

To find a unifying concept for erosion rates, many have turned to stream power. In a precocious effort to understand how running water erodes very weak rock, Howard and Kerby[7] suggested that erosion rates should vary with the stress a flowing stream exerts on its bed, which can be expressed in terms of the discharge and the river gradient, or stream power per unit width. Accordingly, much present work addresses the role of stream power in erosion[8]. Surely the greater the discharge, the faster material can be removed, and abundant evidence shows a correlation of present-day average erosion rates with the steepness of terrain[9,10].

As far as the new work is concerned, Reiners *et al.*[1] and Dadson *et al.*[3] find no correlation between their measured erosion rates and stream power. Burbank *et al.*[2] show that the large variation in rainfall across the Himalaya is compensated to some extent by steeper gradients where rainfall is low, but not sufficiently for them to embrace stream power as the key to account for the poor correlation of erosion rate with rainfall. At the other extreme, Wobus *et al.*[4] exploit the large contrast in stream power between the Greater and Lesser Himalaya as support for the more rapid erosion in one than the other.

Water is Earth's universal solvent, and without it erosion would slow. Yet, as a solution to what makes erosion fast or slow, water's role remains controversial. The differences among these papers call attention to the inadequacy of current theory, without which one gropes for a way to plot data. ■

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Signal transduction

Molecular monogamy

Drew Endy and Michael B. Yaffe

The interactions between cellular proteins must be highly specific, or cells will stop functioning. Some clever protein-manipulation experiments have revealed how this specificity has evolved in yeast.

If an integrated system is to function correctly, its components must be wired together accurately. This requirement presents a particular challenge for living cells, because cellular components move about and intermix, and because the 'wires' themselves are dynamic molecular interactions. In many cells, for instance, protein-based signal-transduction systems are assembled through protein–protein interactions. These interactions are often specified by structurally defined 'domains' in one protein that bind to complementary short, linear amino-acid sequence motifs in another. But even a relatively simple cell such as baker's yeast normally produces more than 4,500 different proteins[1], and frequently several of these proteins contain similar domains or motifs. How, then, do cells wire proteins together with high specificity? On page 676 of this issue, Zarrinpar and colleagues[2] describe one way in which yeast ensures a monogamous protein partnership — by eliminating nonspecific interactions through evolution.

For some types of interaction domains, such as the so-called SH2 and FHA domains, two mechanisms contribute to binding specificity. First, binding occurs only when a particular tyrosine, serine or threonine amino acid in the partner motif has been enzymatically tagged with a phosphate group. The phosphate contributes a large fraction of the total energy required for motif–domain binding[3]. Second, additional amino acids flanking the phosphorylated residue fine-tune the interaction, discriminating between specific and nonspecific partners. But what about other modular domains that recognize more promiscuous motifs, with considerably lower affinity? For instance, how is specificity obtained for SH3 domains, which recognize the core sequence motif proline–X–X–proline (where X is any amino acid)?

This is where the findings of Zarrinpar *et al.*[2] come in. These authors chose to study the interaction between two proteins, Sho1 and Pbs2, from the high-osmolarity glycerol (HOG) signalling pathway in baker's yeast (*Saccharomyces cerevisiae*)[4]. Sho1 is a sensor protein that sits in the membrane of yeast cells and detects changes in external osmolarity. Pbs2 is a signalling protein that coordinates the cellular response to Sho1 activation; the resulting changes in glycerol production help to balance the intracellular and external osmotic pressures. Sho1 and Pbs2 connect through a domain–motif interaction: Sho1 contains an SH3 domain and Pbs2 contains an SH3-binding motif. The SH3 domain in Sho1 is one member of a broader family — there are 27 known SH3 domains in *S. cerevisiae* proteins[2]. But HOG-pathway signalling depends on the specific interaction between Sho1 and Pbs2; cross-reaction with any component from the other 26 SH3-domain–motif pairs could gum up the inner workings of the cell.

Zarrinpar *et al.*[2] start by showing that this doesn't happen (Fig. 1a). They constructed 38 artificial Sho1 proteins by replacing the native Sho1 SH3 domain with one of the 26 other yeast SH3 domains, or with one of 12 such domains taken from multicellular organisms. None of the Sho1 proteins created from the 26 alternative yeast SH3 domains could reconstitute HOG-pathway function *in vivo*. Curiously, however, six of